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Abstract

Electrobaissoptera liui sp. nov., a new species of the snakefly family Bassopteridae, is described and figured from an individual preserved in mid-Cretaceous amber from Tanai, northern Myanmar. *Electrobaissoptera liui* sp. nov. preserves nearly all of the known characters used to circumscribe the family and genus, and is unique among bassopterids for possessing a complete ma-mp crossvein in the hind wing, thereby dividing cell m1.

Keywords: Cenomanian; New species; Paleodiversity; Systematic

1. Introduction

Species of the order Raphidioptera, most frequently known as snakeflies, are easily distinguished from other holometabolous insects owing to the combination of a prognathous head, a slender and elongate prothorax, the presence of a pigmented pterostigma, and a long ovipositor. As larvae, with a terrestrial life-style, they may be recognized by their elongate flattened body, a prognathous head with chewing-mandibulate mouthparts, and a soft 10-segmented abdomen. Adults and larvae are known to be entomophagous and/or necrophagous, with larvae living under tree bark, and amid detritus around the roots of shrubs (Kovarik et al., 1991; Aspöck, 2002). Some adults have been observed feeding on pollen (Aspöck and Aspöck, 2009). Most remarkably and unique among homometabolan insects, snakeflies have active pupae, with dectitious mouthparts, and are predators of small arthropods (Engel et al., 2018).

The Raphidioptera, together with Megaloptera and Neuroptera, comprise the superorder Neuropterida, which has been presumed to have first diverged from other early Holometabola during the Late Carboniferous (Vasilikopoulos et al., 2020). This estimate seems to agree with the age of the oldest putative stem-representatives of the superorder dated to the Permian (e.g., Shcherbakov 2013). The oldest definitive Raphidiidae and Inocelliidae (the two extant families) are from Eocene, even if an enigmatic taxon, *Sinoinocellia liaoxiensis*, was described as an inocelliid from the Callovian of China (Wang, 1987). *Sinoinocellia* was poorly documented and needs to be critically reevaluated. However, the Early Cretaceous age proposed by Vasilikopoulos et al. (2020) for crown-Raphidioptera is an illustration of the discrepancies between node-dating estimates and stratigraphic/fossil evidence. The 'time divergence estimate using node-dating' method that Vasilikopoulos et al. (2020) employed, only allows for the integration of families with extant representatives, which is a minor part of snakefly diversity (25% of familial diversity, or even less if Mesoraphidiidae are paraphyletic, and definitively much less at the specific level). Therefore, Vasilikopoulos et al. (2020) dated a potential divergence

time for the families Inocelliidae and Raphidiidae (i.e., Neoraphidioptera), rather than Raphidioptera. This is further complicated if Neoraphidioptera are polyphyetic, as one hypothesis considers Inocelliidae and Raphidiidae to have originated separately from among clades of Mesoraphidiidae or other Cretaceous snakeflies (e.g., Lu et al., 2020). To offer consistent dating, only a tip-dating or total-evidence dating approach would make it possible to properly consider the entire fossil record of the order, and to propose ages that are more reflective of the true paleontological diversity of the lineage (Jouault et al., 2021a,b). Nevertheless, putative representatives of stem-group Raphidioptera have been recorded from deposits as early as the Permian (Shcherbakov, 2013; Engel et al., 2018) suggesting that the order is at least of Permian age. During the Mesozoic, the order was speciose (e.g. Lu et al., 2020) and widely distributed (http://fossilworks.org/), but it declined rapidly prior to and after the Cretaceous/Cenozoic (K/T) event. The mid-Cretaceous amber from Myanmar provides important insight into their diversity and morphology prior to this decline. Herein, we describe and figure a new species of snakefly from this rich deposit.

2. Material and methods

The amber piece containing the specimen comes from the deposits of Noije Bum in the Hukawng Valley (26° 29′ N, 96° 35′ E), Kachin State, northern Myanmar (see detailed map in Grimaldi and Ross, 2017: fig. 2). Radiometric data established an early Cenomanian age (98.79 ± 0.62 Ma) for Kachin amber, based on zircons from volcanic clastes found within the amber-bearing sediments (Shi et al., 2012). Some ammonites found in the amber-bearing bed and within the amber itself corroborate a latest Albian–earliest Cenomanian age (Cruickshank and Ko, 2003; Yu et al., 2019).

The holotype of *Electrobaissoptera liui* sp. nov. is nearly complete, only damaged at the apices of the left wings and abdomen. The amber piece was polished using a polisher (Buehler EcoMet 30) and a thin silicon carbide sanding paper (grit size = 7000), and the specimen was examined and photographed with a Leica MZ APO with an attached Canon EOS 5D Mark II camera. All images were digi-

tally stacked photomicrographic composites of several individual focal planes, which were obtained using Helicon Focus 6.7. The figures were composed with Adobe Illustrator CC2019 and Photoshop CC2019. The wing venation and cell nomenclature follows Lu et al. (2020). The amber piece is housed in the amber collection of the Geological Department and Museum of the University of Rennes, France (IGR).

This published work and its new nomenclatural act are registered in ZooBank with the following LSID (reference): urn:lsid:zoobank.org:pub:XXXX

3. Systematic Paleontology

Order Raphidioptera Navás, 1916

Suborder Raphidiomorpha Engel, 2002

Family Baissopteridae Martynova, 1961

Genus *Electrobaissoptera* Lu et al., 2020

Included species: *Electrobaissoptera burmanica* Lu et al., 2020 (type species); *Electrobaissoptera liui* sp. nov.

Electrobaissoptera liui sp. nov.

Figs. 1–3

Lsid: XXXX

Type material. Holotype: IGR.BU-028 deposited in the Geological Department and Museum of the University of Rennes, France (IGR) (in an amber piece measuring 20 × 16 × 5 mm, with several minute syninclusions and an orthopteran nymph *plus* a platypodid beetle).

Locality and horizon. Noije Bum Hill, Hukawng Valley, Kachin State, Myanmar; upper Albian to lower Cenomanian, mid-Cretaceous.

Etymology. The specific epithet honors Prof. Xingyue Liu (College of Plant Protection, China Agricultural University, Beijing) for his copious and superb contributions to our understanding of Neuropterida.

Diagnosis. Tarsomere III symmetrically bilobed, with a pair of wide lobes; forewing long elliptical, ca. 3.25× as long as wide; pterostigma ca. 6.0× as long as wide; RA simple distad pterostigma; hind wing with cell m1 divided into two parts by a complete ma-mp crossvein.

Description. Body length ca. 6.39 mm (as preserved); antenna length ca. 3.24 mm; forewing length ca. 6.69 mm and width ca. 1.99 mm; hind wing partially preserved.

Body dark brown without distinctive color pattern (Fig. 1); head narrowly rectangular, with vertex slightly longer than compound eye; occiput short; compound eyes ovoid, exophthalmic; ocelli present (Figs. 1; 2A). Prothorax slender, elongate, slightly longer than head; meso- plus metathorax as long as prothorax. Legs slender, densely covered with microtrichia; tarsomere III symmetrically bilobed, with a pair of slender lobes (Fig. 2B); pretarsal claws forked at distal third, with an acutely tapering inner ramus (Fig. 2B). Forewing long elliptical, ca. 3.25× as long as wide (Figs. 1A,C; 3A); costal space broadened at proximal third, with five simple crossveins; ScP terminating into costal margin slightly distad wing midpoint; four simple RA veinlets present; pterostigma ~6.0× as long as wide, uniformly colored, closed by a crossvein proximally, distally ending at second veinlet of RA, with a straight but distinctly inclined incorporated veinlet of RA; three radial crossveins present, three radial cells gradually shortened, r1 longest, r2 broadest; RP forked proximad its midpoint, with two simple branches; two rp-ma crossveins, forming two discal cells; MA with stem originating at MP1, distinctly distad initial branching point of MP; MA deeply forked proximad its midpoint, with two simple branches, length of branching of MA as long as branching of RP; three ma-mp crossveins, forming three medial cells; MP deeply forked, with three terminal branches and a series of three discoidal cells; CuA marginally forked; CuP simple; two cua-cup crossveins present; A1 and A2 simple. Hind wing slightly shorter and narrower than forewing (Figs. 1A; 3B); costal space narrow, with five crossveins; ScP terminating into

costal margin slightly proximad wing midpoint; four simple RA veinlets present; pterostigma similar to that of forewing; five radial crossveins present, r3 longest and broadest, remaining radial cells almost of equal lengths; RP forked proximad its midpoint, with two simple branches; two rp-ma crossveins, forming two discal cells; MA with stem originating from base of MP stem, long and sinuate; MA forked at its midpoint, with two simple branches, branching of MA as long as branching of RP; four ma-mp crossveins, forming three medial cells; MP deeply forked, with four terminal branches and a series of three discoidal cells; cell m1 divided into two parts (m1a and m1b on the drawing) by a ma-mp crossvein, directed toward stem of MA; three mp-cua crossveins, with 1mp-cua almost vertical to stem of MP; CuA distally forked; CuP simple; two cua-cup crossveins present; A1 and A2 simple. Terminalia not preserved.

4. Discussion

The order Raphidioptera was quite diverse during the Mesozoic, with numerous genera and species described from amber inclusions and compression fossils (e.g., Lyu et al., 2017a,b; Lu et al., 2020). This diversity has been organized into six extinct families Priscaenigmatidae, Chrysoraphidiidae (perhaps best considered a subfamily of the former family), Juroraphidiidae, Baissopteridae, Mesoraphidiidae, and Metaraphidiidae (also perhaps best classified as a subfamily of the preceding family) (Liu et al., 2014). The present fossil cannot be placed among the Priscaenigmatidae (*sensu* Engel, 2002) owing to the presence of a broad costal area (vs. narrow); a short Sc that does not extend to the wing apex, and fuses into C near the wing midpoint (vs. extending nearly to the wing apex before fusing with R); a different configuration of CuP; and a distinct 'ovoid', basal cell between A1 and A2 (vs. absent) (Whalley, 1985: figs. 45–46). Similarly, the present specimen cannot be placed in Chrysoraphidiidae as diagnosed by Liu et al. (2013) owing to the possession of a simpler wing venation (i.e., fewer radial cells and ScA not present); a short closed pterostigma (vs. elongate, open proximally, closed distally by veinlet of R); Sc meeting C before the pterostigma (vs. running within the pterostigma to its distal end, connecting to

R by a distal oblique crossvein); MA branching (vs. simple); crossveins not arranged in two series of gradate crossveins in the radial and mediocubital fields (vs. arranged as stated); A1 short and simple (vs. long, pectinately branched, with two branches). The current fossil cannot be placed in Juroraphidiidae (as defined by Liu et al., 2014) due to the more complex wing venation (i.e., with numerous cells and three discoidal cells); a relatively wide costal region (vs. narrow); the tarsi tetramerous, with tarsomere III bilobed (vs. pentamerous and tarsomere III simple); a short closed pterostigma (vs. elongate, open proximally); a short Sc, terminating before the pterostigma (vs. long, running within the pterostigma); and forewing MA forked (vs. simple). The fossil does not fall within Mesoraphidiidae as circumscribed owing to the presence of ocelli (vs. absent or rarely present) (Liu et al., 2016: figs 2, 5, 7); a more developed wing venation (i.e., with three cells doi, two cells dc; a pterostigmal RA veinlet, vs. absent); pretarsal claws with a pre-apical ramus (vs. simple). The family Metaraphidiidae was proposed by Bechly and Wolf-Schwenninger (2011) to accommodate the peculiar genus *Metaraphidia* Whalley, 1985. They used the following forewing venation characters in the diagnosis of the family: pterostigma divided by two crossveins; A2 and A3 not fused; no crossvein between CuA and CuP. Our specimen does not possess such wing venation since only one RA veinlet is present in the pterostigma, and more importantly CuA and CuP are connected by a crossvein, while their absence in *Metaraphidia* is considered to be an apomorphic character of the family. In actuality, Metaraphidiidae is likely merely an autapomorphic member of the Mesoraphidiidae as there are no convincing synapomorphies for mesoraphidiids excluding *Metaraphidia*. Metaraphidiidae should be seriously reevaluated as either considered a subfamily of Mesoraphidiidae or synonymized outright.

Recently, Lu et al. (2020) revised the diagnosis of the family Baissopteridae and proposed the following characters to differentiate the family: ocelli present; RA veinlet within pterostigma usually present; forewing M with stem usually shorter than doi1; forewing M and CuA diverging at an angle of more than 40°; venation enriched, especially crossvenation, forming at least three radial cells in the forewing and four radial cells in the hind wing, at least two discal cells in both fore- and hind wings,

usually four or more discoidal cells in both fore- and hind wings; male gonocoxites IX paired and shell-like; male gonapophyses IX reduced. All of these wing venational and body characters are present in the present fossil, with the exception of those genital characters as these cannot be observed owing to the incomplete preservation of the specimen. Therefore, it is clear that the current fossil belongs to the family Baissopteridae.

Following the key to genera of Baissopteridae of Lu et al. (2020), the present fossil keys out to the genus *Electrobaissoptera* Lu et al. 2020 owing to the hind wing with the stem of MA long, slightly sinuate; the head with normal-sized compound eyes and a well-developed vertex; the hind wing cell doi1 with a crossvein directed toward or connecting to the stem of MA; the generally small body size, with forewing 5.5–7.0 mm long; the forewing RP with only two branches; the forewing MA separating from MP obviously distad the initial branching point of MP; and with RP branches almost as long as MA branches in the forewings.

The new specimen is relatively small with a forewing about 6.70 mm (compared to most other Baissopteridae with wings longer than 15 mm), thereby excluding affinities with other Burmese amber genera (e.g., *Allobaissoptera* Lu et al., 2020); the head is narrowly rectangular, but its exact width is unknown (the amber piece cannot be prepared for a direct dorsal view due to the position of syninclusions); and the vertex is nearly as long as the compound eye (diameter of compound eye about one-third head length). All of these characters fit well with those of *Electrobaissoptera burmanica* Lu et al., 2020, even if the place occupied by the compound eyes and their lengths differ. However, the present fossil differs from *E. burmanica* in tarsomere III symmetrically bilobed, with a pair of wide lobes, rather than slender in *E. burmanica* (Lu et al., 2020: fig. 11e); forewing long elliptical, ca. 3.25× as long as wide, vs. 3.5× as long as wide; pterostigma ca. 6.0× as long as wide, vs. 5.0× as long as wide; RA simple distad pterostigma vs. forked in *E. burmanica*; hind wing with cell m1 divided into two parts by a complete ma-mp crossvein, vs. incomplete in *E. burmanica* (Lu et al., 2020: fig. 12d-e). Notice that the two veins are less pigmented than the surrounding veins but clearly present. Although several dif-

ferences are recorded between *E. burmanica* and the current fossil, these are more trivial features and not suggestive of distinct genera but instead closely related species. The venation of *Electrobaissoptera liui* sp. nov. is not aberrant (and certainly not teratological), and demonstrates that Baissopteridae may display several intermediates in wing venation with species lacking or possessing a rudimentary or complete ma-mp crossvein. Nonetheless, given the general rarity of these fossils it is not possible to critically evaluate potential ranges of morphological variation within any given fossil species. Based on observed variations in modern snakeflies, albeit of different families from those in the Mesozoic, the observed differences in wing venation between the current fossil and other baissopterids certainly suggests separate species rather than extremes of a range of population variation.

5. Conclusion

Amber from northern Myanmar provides once again novel insights into the paleodiversity of the West Burma Block (WWB) during its break-up and migration from South Gondwana to Asia during the Cretaceous. The description of *Electrobaissoptera liui* sp. nov. serves to increase the diversity of baissopterid documented from the WWB during the mid-Cretaceous and helps to clarify some wing venation characters originally presumed to be potential aberrations in *E. burmanica*. If the fossil record of the order continues to grow, it seems obvious that a phylogeny integrating the whole of the fossil diversity of Raphidioptera will be needed to clarify the classification and estimate times of divergence among the various clades, and ultimately to propose clear hypotheses concerning snakefly diversification and eventual and decline.

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297 Figure 1. *Electrobaissoptera liui* sp. nov., holotype IGR.BU-028. A: Habitus in left lateral view; B: De-
298 tailed view of head; C: Detailed view of forewing. Scale bars equal 0.5 mm.
299 Figure 2. Detailed view of *Electrobaissoptera liui* sp. nov., holotype IGR.BU-028. A: Head with black
300 arrows pointing ocelli; B: Mid-legs with black arrow pointing the pre-apical ramus. Scale bars equal
301 0.25 mm
302 Figure 3. Line drawing of wing venation with cell and vein names labelled. A: Forewing; B: Hind wing.
303 Scale bars equal 0.5 mm.

A

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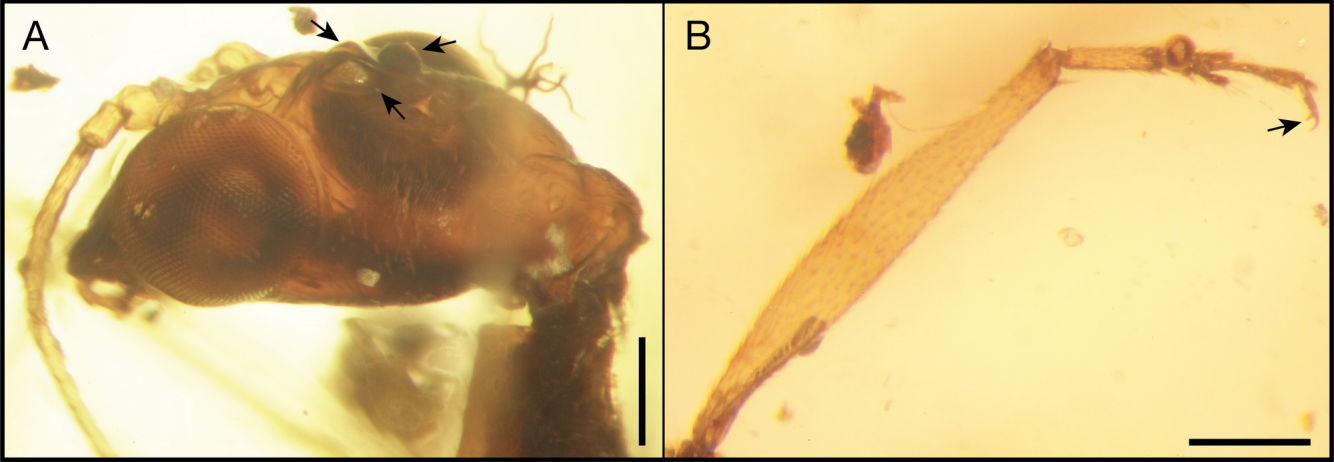
C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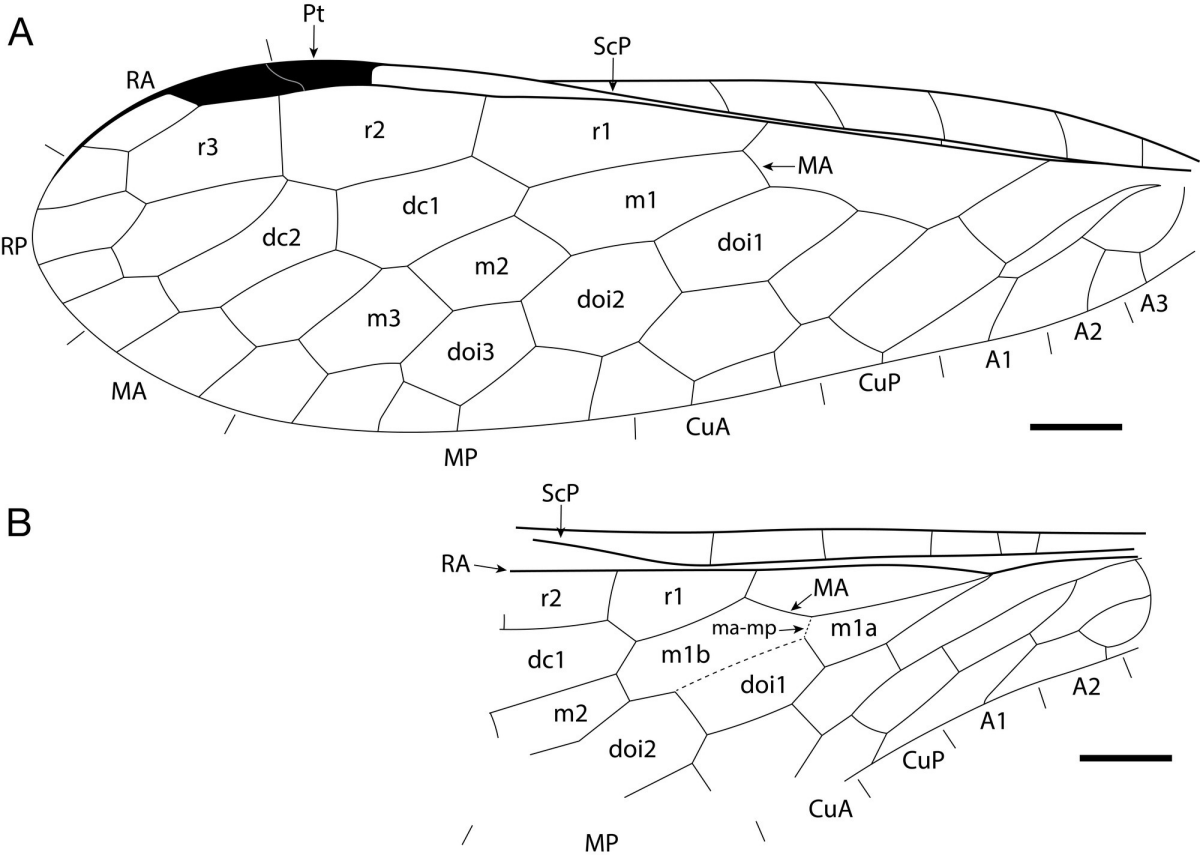
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